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Summary

This study is part of an ongoing collaborative research effort between the Life Science and Human Factors Divisions at NASA Ames Research Center to measure the accuracy of human motion perception in order to predict potential errors in human perception/performance and to facilitate the design of display systems that minimize the effects of such deficits. The study describes how contrast manipulations can produce significant errors in human speed perception. Specifically, when two simultaneously presented parallel gratings are moving at the same speed within stationary windows, the lower-contrast grating appears to move more slowly. This contrast-induced misperception of relative speed is evident across a wide range of contrasts (2.5 – 50%) and does not appear to saturate (e.g., a 50% contrast grating appears slower than a 70% contrast grating moving at the same speed). The misperception is large: a 70% contrast grating must, on average, be slowed by 35% to match a 10% contrast grating moving at 2°/sec ($N = 6$). Furthermore, it is largely independent of the absolute contrast level and is a quasilinear function of log contrast ratio. A preliminary parametric study shows that, although spatial frequency has little effect, the relative orientation of the two gratings is important. Finally, the effect depends on the temporal presentation of the stimuli: the effects of contrast on perceived speed appears lessened when the stimuli to be matched are presented sequentially. These data constrain both physiological models of visual cortex and models of human performance. We conclude that viewing conditions that effect contrast, such as fog, may cause significant errors in speed judgments.

Introduction

The coding of speed and direction within the visual system has long been a focus of research for visual neuroscientists. Impressive progress has been made in our understanding of direction coding, but speed coding remains largely a mystery. The generally accepted

description is as follows. Direction information is retained using a place code with the direction of stimulus motion given by *which* cell is firing most vigorously within an ensemble of neurons. Each neuron would act as a detector labeled for a particular direction of motion within a spatial map of all possible directions. This idea is strongly supported by the finding of a neatly organized array of direction columns within the middle temporal cortex (MT), an area of visual cortex known to be involved in motion perception (Albright, Desimone, and Gross 1984; Newsome et al. 1985; Newsome, Britten, and Movshon 1989; Salzman, Britten, and Newsome 1990). Since no such spatial organization has ever been found for speed-tuning, one possibility is that speed information is encoded by the neuronal firing rate. However, because the firing rate of individual visual cortical neurons is not uniquely related to speed (see Maunsell and Newsome 1987), stimulus speed would have to be encoded by the collective firing rate of an ensemble of neurons. The details of such a scheme have yet to be worked out.

Physiological studies have shown that the response of most neurons within the visual cortex increases monotonically with increasing stimulus contrast (e.g., Albrecht and Hamilton 1982; Sclar, Maunsell, and Lennie 1990). As long as the neurons have similar contrast sensitivities, this contrast response is not a problem for a direction-coding scheme that uses peak response within a population of neurons to determine direction. However, contrast variations present a significant obstacle to any speed-coding scheme that uses neuronal firing rate to encode speed information. Any such scheme must include a mechanism to disambiguate speed and contrast information.

The basic problem of how to distinguish neuronal responses related to contrast from those related to speed has been a major concern of both physiologists and modelers. Various mechanisms have been proposed to achieve contrast-independent measures of speed (Watson and Ahumada 1985; Adelson and Bergen 1986; Heeger 1987; Grzywacz and Yuille 1990), but an early study of the effect of contrast on the perceived speed of moving gratings showed that perceived speed is actually affected by contrast. Using the method of adjustment and magnitude estimation, Thompson (1982) found that, at least below

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8 Hz, a lower-contrast grating appears to move more slowly than a higher-contrast grating moving at the same speed. Unfortunately, he examined only a limited range of contrasts (at and below 17.8%). In apparent conflict with this result, a study of grating-speed discrimination (McKee, Silverman, and Nakayama 1986) found no effect of random trial-by-trial variations (from 5 – 82%). This second result suggested that speed is veridically coded and cleanly disambiguated from contrast variations. The issue was revived after a recent finding that the direction of a moving plaid (the sum of two sinusoidal gratings of different orientation), whose components have different contrasts is biased by up to 20° in the direction of motion of the higher-contrast component (Stone, Watson, and Mulligan 1990). This bias can be explained if component speed is misperceived as predicted by Thompson (1982). To reconcile these discrepancies, we reexamined the contrast effect on the perceived speed of moving gratings over a wide range of contrasts using a two-alternative forced-choice paradigm. Preliminary reports have appeared elsewhere (Thompson and Stone 1990; Stone, Thompson, and Watson 1990).

Methods

Experimental procedures

Subjects were asked to perform two types of psychophysical judgments: speed-matching and direction-discrimination. In the first task, we measured the perceived relative speed of two grating patches of identical spatial frequency, but of different contrast. For comparison, in the second task we measured the perceived direction of a moving plaid that consisted of component gratings of identical spatial frequency, but of different contrast.

In the first set of experiments (figs. 1–5), we measured the perceived relative speed of two *simultaneously* presented, horizontal drifting gratings. The stimulus consisted of two horizontally elongated grating patches centered either 1.3° above or below the fixation cross at the center of the image. For the 70% test-contrast experiments, the x and y standard deviations of the Gaussian window were 0.71° and 0.36°, respectively. For the 20% and 40% test-contrast experiments, the x and y standard deviations were 0.95° and 0.48°. Subjects were presented with a single stimulus interval, during which both gratings drifted upward. They were asked to ignore contrast and to indicate in a two-alternative forced choice, whether the top or bottom grating appeared to move faster. The standard grating moved at 2°/sec. The speed of the test was changed within two interleaved up-down staircases. The

test was randomly located in either the upper or lower position.

In a second set of experiments, we made a preliminary assessment of the effect of relative orientation/direction on contrast-induced speed-matching errors (fig. 6). The stimuli consisted of two gratings viewed through circularly symmetric Gaussian windows (standard deviation = 0.36°) located 1.3° above and below the fixation point. In one experiment (fig. 6 and data used to generate the predictions in figs. 7(a) and 7(b)), one grating was oriented horizontally and the other vertically. In another experiment (data used to generate the predictions in figs. 7(c) and 7(d)), one grating normal was oriented 60° to the right of vertical while the other was oriented 60° to the left. In both of these experiments, which of the two orientations appeared in the upper and lower window was randomized (two possible spatial arrangements). Subjects were presented with a single interval, during which both gratings drifted perpendicular to their orientation in a random direction: for the orthogonal gratings, either left/right or up/down (four possible combinations per spatial arrangement), while for the gratings oriented 120° apart, either both upward or both downward (two possible combinations per spatial arrangement). The standard patch (randomly either orientation and either location) moved at 2°/sec while the test-patch speed was determined by two interleaved up-down staircases. Subjects were asked to ignore all other factors (contrast, orientation, and direction) and to respond in a two-alternative forced choice which patch (top or bottom) moved faster.

In a third set of experiments using a previously established protocol (Stone, Watson, and Mulligan 1990), we measured the effect of contrast on the perceived direction of moving plaids consisting of components with different contrasts (fig. 7). The plaid consisted of the sum of two superimposed gratings of different orientations viewed through a single stationary circularly symmetric Gaussian window (standard deviation = 0.95°) and centered on the fixation point, which was extinguished during the actual stimulus presentation. The components were either orthogonal (normal vectors 45° off vertical) or 120° apart (normal vectors 60° off vertical). Therefore, the differences between the plaids in this set of experiments and the grating-pair stimuli in the previous set were the location of the grating patches, the absolute orientation of the gratings, whether or not they were superimposed, and the size of the stimulus patches. Subjects were presented with an upward-moving plaid and asked to respond in a two-alternative forced choice whether the plaid appeared to move to the right or left of straight up. The actual direction of the plaid was determined by two interleaved up-down staircases and was achieved by changing the

speed ratio of the two components while keeping component orientation and plaid-speed constant.

In the last experiment, we measured the effect of contrast on the perceived relative speed of *sequentially* presented horizontal drifting grating patches (fig. 8). Subjects were presented with two stimulus intervals. Each interval consisted of two horizontally elongated grating patches of identical contrast centered either 1.3° above or below the fixation cross at the center of the image. In one interval (standard), both gratings moved upward at exactly $2^\circ/\text{sec}$. In the other interval (test), both gratings moved upward at the same speed determined by two interleaved up-down staircases. The test and standard intervals were presented in random order. Subjects were asked to ignore contrast and to respond in a two-alternative forced choice whether the gratings appeared faster in the first or second interval.

All stimulus intervals were 500 milliseconds (ms). The contrast rose with a Gaussian time course reaching full contrast after 50 ms, stayed at full contrast for 400 ms, then fell with the same Gaussian time course over the final 50 ms.

We used eight observers (six were naive to the experiment purpose) between 16 and 40 years old. Subjects viewed the screen binocularly through natural pupils from a distance of 273 cm. The image subtended $5.4^\circ \times 5.4^\circ$ (20 pixels/cm) and the mean luminance of the image was 75 cd/m^2 .

Control for Size and Duration

Because the Gaussian-tapered spatial and temporal windowing links change in stimulus contrast to change in perceived stimulus size and duration, we repeated some of the experiments in two subjects (including one naive subject) using sharp circular spatial windows and sharp temporal onset and offset. The results were qualitatively unchanged. The contrast manipulations, not the concomitant small changes in size and duration, were responsible for the speed-matching errors of these two subjects. Therefore, it is unlikely that the effects described for the other subjects and the other experiments are due to size or duration changes associated with our contrast manipulations.

Data Analysis

The staircase method yielded typical psychometric curves (fig. 1). We fit the data for each condition with a cumulative Gaussian using a weighted least-squares procedure (Mulligan and MacLeod 1988) based on probit analysis (Finney 1971). For the speed-discrimination tasks, the inflection-point location represents a bias that we refer to

as the *speed match* (the test-grating speed that is perceived equal to that of the standard). The speed match is expressed as a percentage of the standard speed. We define the *speed error* as the percent error of the speed match compared to the standard speed. The standard deviation of the best fitting cumulative Gaussian is a measure of the precision in the observer's judgments which we plot as *speed uncertainty* (the ratio of the standard deviation of the psychometric curve to the standard speed is divided by $\sqrt{2}$ because we assume equal uncertainty for the test and standard gratings). For the plaid-direction discrimination task, the location of the inflection point (bias) is the direction of plaid motion that is perceived as straight upward. This bias, obtained by manipulating the speed ratio, is the exact negative of the *direction error* perceived when the plaid is moving straight, assuming the direction error is caused by an underlying inequality in the perceived component speeds (Stone, Watson, and Mulligan 1990).

Stimulus Generation

We generated the drifting grating patches and plaids on a Mitsubishi 19-inch high-resolution monochrome monitor (model M-6950) using an Adage RDS 3000 image display system. The monitor luminance was corrected for its gamma nonlinearity using a lookup table procedure described in Watson et al. (1986). A detailed analysis of the animation procedure is in Mulligan and Stone (1989) and the procedure was previously used to generate moving plaids (Stone, Watson, and Mulligan 1990).

The stimulus was a $512 \text{ pixel} \times 512 \text{ pixel}$, 8-bit/pixel image created using both locally developed programs and the Human-Information-Processing-Laboratories Image Processing System (HIPS) image-processing software package (Landy, Cohen, and Sperling 1984). In some experiments (for all plaids and gratings with 20% and 40% test contrasts), four two-dimensional (2-D) sinusoidal gratings were generated (sine- and cosine-phase components for each grating patch). These four images were multiplied by a 2-D Gaussian to provide windowing without sharp edges. The images were then halftoned using a modified error-diffusion method (Floyd and Steinberg 1975; Mulligan 1986). The four resulting bit-mapped images were loaded into the four lower-order bit-planes. A $3 \text{ pixel} \times 3 \text{ pixel}$ white fixation cross was drawn into a fifth bit-plane in the center of the image. The remaining three bit-planes were blank. The image was loaded into the framebuffer within a few seconds. Then, by varying the lookup table on a frame-by-frame basis (at 60 Hz), we modulated the contrast of the sine- and cosine-phase components of each grating in temporal quadrature so they appeared as a single drifting grating. Using this

method, we had complete control over the speed and contrast of both gratings without having to load new images into the framebuffer. Furthermore, the initial spatial phase of each grating was randomized so that using position cues to assess motion would be difficult. A different base image was necessary for each of the different spatial-frequency stimuli used.

In some experiments (70% test contrast), we used a modified procedure for two reasons: at high contrast, halftoning at 1 bit/pixel produced visible noise and the method described above did not allow the generation of a total contrast (sum of both grating contrasts) above 71%. To reduce the halftoning noise and increase contrast resolution, we halftoned each grating image down to 2 bits/pixel using the same error-diffusion algorithm. To increase the maximum attainable contrast, we constructed two half images so that each could be as high as 71%. Two 4-bit half-images (256 pixel \times 512 pixel) were generated with each containing two 2-bit halftoned sine- and cosine-phase components of a grating patch. The two upper and lower half-images were combined to generate a 512 pixel \times 512 pixel image. A 1-bit mask was put into the fifth bit-plane of the upper half of the image to allow separate animation of the upper and lower patches. A fixation cross was put in the sixth plane at the center of the image. Animation was achieved by modifying the lookup table on a frame-by-frame basis. The principles behind these modifications are described in detail in Mulligan and Stone (1989).

Results

When two drifting grating patches are presented one above the other, the lower-contrast grating appears to move more slowly than an otherwise identical higher-contrast grating moving at the same actual speed. Figure 1 plots typical raw psychometric curves for one subject under three different stimulus conditions. The center curve was generated in response to stimulus presentations where both gratings were 70% contrast. The leftmost curve was generated with a 70% contrast test grating and a 10% standard grating. The rightmost curve was generated with a 10% test grating and a 70% standard grating. In all three cases, the standard moved at 2°/sec. When the contrasts were identical, the subject made veridical matches with the inflection point at 1.97°/sec yielding a speed match of 98.5% or a speed error of 1.5%. However, when the contrast of the test was higher (leftmost curve), the inflection point was at 1.71°/sec (85.5% speed match, 14.5% error). Conversely, when the contrast of the test was lower (rightmost curve), the inflection point was at 2.34°/sec (117% speed match, 17% error).

Five out of the six subjects tested with simultaneously presented pairs of moving grating patches consistently reported the lower-contrast grating as moving more slowly. Figure 2 plots the speed match for six subjects as a function of the contrast ratio in decibels (dB) ($20 \log_{10}$ of the ratio of the standard contrast to the test contrast). For the four leftmost points, the test grating was always 70% and the standards were 10, 30, 50, and 70% contrast, starting from the left. For the three leftmost points (10, 30, and 50% contrast standards), the test needed to be slowed by as much as 45% to appear to drift at the same rate as the standard. The upward arrows indicate that, for the five subjects that showed the effect, even a 50% contrast standard appeared to move more slowly than the 70% contrast test. The perceived speed difference was significant for four subjects ($p < 0.05$ in one-tailed t -test). This result suggests that the effect occurs over the entire range of contrasts. When the standard and test were both 70%, all six subjects made veridical matches. For the rightmost point, the test was 10% and the standard was 70% contrast. In this case, the same five subjects matched speeds when the test was up to 51% faster than the standard. This indicates that the two symmetric methods for measuring the effect (slowing the higher contrast grating or speeding up the lower contrast grating) yielded similar results.

The effect on perceived speed appears quasilinear in log contrast. On average, the six subjects mismatched speed by 30% when matching 70% and 10% contrast gratings. Furthermore, the data in figure 2 are fit remarkably well by simple straight lines for all subjects (mean slope = 1.5% bias/dB; mean intercept = 98.6%; mean correlation coefficient = 0.958). Even for the one subject for whom the effect appears weak or nonexistent (fig. 2(f)), the correct trend—positive slope—is still present).

Speed discrimination (the ability to distinguish small differences in speed) is not systematically affected by contrast under the same conditions that produce matching errors. Although the three curves in figure 1 are shifted with respect to each other, they have similar slopes. The speed uncertainties are 4.5, 7.0, and 7.5% for the center, left, and right curves, respectively. Figure 3 plots speed uncertainty as a function of contrast ratio for the same six subjects and the same stimuli. Although for some subjects there was a slight tendency for higher uncertainty at higher contrast ratios, there is no clear and systematic relationship between the precision of the match and contrast ratio. Therefore, although subjects are consistently mismatching speed by up to 50% when the contrasts are different, they are doing so with similar levels of uncertainty regardless of relative contrast.

Speed-matching errors were not affected by changing the absolute contrast level. Three subjects (one naive) were

tested with more than one test contrast. The lefthand panels of figure 4 plot results when 70, 40, and 20% contrast test gratings were slowed to match lower contrast gratings. For all three subjects, the data nearly superimpose. The right panels of figure 4 plot the results when 10% and 2.5% contrast test gratings were increased in speed to match higher contrast gratings. It is clear that for all three subjects the speed error data point for the 10% test is nearly identical to the corresponding points in the lefthand panels. However, at 2.5% test contrast, for all three subjects the speed errors appear larger at a given contrast ratio than those in the lefthand panels. These data indicate that, at least for test contrasts at or above 10%, the contrast-induced speed-matching error is a function of the contrast ratio alone and is largely insensitive to differences in absolute contrast. At and below 2.5% test contrast, the effect may be larger.

Speed-matching errors were not sensitive to small changes in temporal and spatial frequencies. The same subjects as in figure 4 were tested at two different spatial/temporal frequencies (fig. 5). For all three subjects, the effect is remarkably similar for a 1.5 cycle/degree (c/d) grating moving at 2°/sec (3 Hz) and for a 3 c/d grating moving at 2.75°/sec (8.25 Hz). These data show that a two-fold change in spatial frequency and a nearly three-fold change in temporal frequency have little effect on the contrast-induced errors in perceived relative speed. Even higher temporal frequencies were tested with two subjects. One subject (fig. 5(a)) continued to show the contrast-induced errors even at 10 Hz, while a second subject (fig. 5(b)) could not perform the task above 8.25 Hz. Finally, two subjects were tested at 8.25 Hz at two different test contrasts (35% and 70%). As with the data at the lower temporal frequency (fig. 4), the effect was nearly identical at the two absolute contrast levels. Therefore, at least over the range tested, spatial and temporal frequency as well as absolute speed has little effect on the contrast-induced misperception of relative speed.

The effect of contrast on perceived speed is sensitive to the relative orientation of the gratings. Figure 6 plots the results of the three subjects (including one naive) who were tested in conditions where the upper and lower gratings were orthogonal. The effect of contrast on perceived relative speed appears different from when the gratings were parallel (figs. 2 and 4). The effect showed greater intersubject variability, evidence of saturation, and dependence on absolute contrast. For one subject (fig. 6(a), PT), the lower contrast gratings still appear slower although the effect was greater at lower absolute contrast. For a second subject (fig. 6(b), LS), the effect is gone (compare open squares in figs. 4(b) and 6(b)) and speed matches are essentially veridical except at high contrast ratios and low

absolute contrast. For the third subject (fig. 6(c), JC), the results are less clear. Saturation is suggested by the fact that not one of the three subjects showed a significant difference in the perceived speed of a 70% test and a 50% standard when tested with orthogonal gratings (see downward arrows in fig. 6), while four of six subjects showed a significant difference when tested with parallel gratings (fig. 2). Furthermore, for the two subjects tested with a 20% contrast test and a 10% contrast standard under both the parallel and orthogonal conditions (PT and LS), both made significant speed-matching errors in the parallel condition ($p < 0.05$; figs. 4(a) and 4(b)) but not in the orthogonal condition (figs. 6(a) and 6(b)). Finally, at high contrast ratios, all three subjects showed a stronger effect using the 20% contrast test. We conclude that the relative orientation of the gratings affects the contrast-induced misperception of relative speed.

Stone, Watson, and Mulligan (1990) showed that the relative contrast of the grating components within a plaid affected its perceived direction of motion. They reasoned that a contrast-induced misperception of component speed was responsible. If the error in perceived component speed is fed into a mechanism that reconstructs plaid velocity from component information, plaid motion would be misperceived in a quantitatively predictable manner. If the reconstruction is achieved using the intersection of perpendicular constraints rule (Fennema and Thompson 1979; Adelson and Movshon 1982), the error in perceived plaid direction (Δ) is related to the perceived ratio of the component speeds (R) by the following equation:

$$\Delta = \arctan\left(\frac{R-1}{R+1} \cotan \frac{\theta}{2}\right) \quad (1)$$

with θ being the angle between the directions of motion of the two components.

We predicted the effect of contrast on the perceived direction of a moving plaid from contrast-induced biases in grating speed in two subjects. The predicted direction error was generated using equation (1), the known θ , and the measured R in the same subjects. Figure 7 shows the actual and predicted responses. Although the subjects performed differently, the actual performance for both of them in the plaid-direction task (squares) is well predicted by equation (1), using their own grating speed-matching data (dashed line).

Individual subjects showed distinct differences in their performance when tested with non-parallel gratings. Specifically, the two subjects tested with plaids showed significant differences in their speed matching when

presented with orthogonal gratings. Subject PT still showed a significant contrast-induced misperception of relative speed (fig. 6(a)), while subject LS did not (fig. 6(b)). The same dichotomy was found in their perception of moving plaids. Subject PT showed a large error in the perception of plaid direction (fig. 7(a)) while subject LS did not (fig. 7(b)). The variability in grating-speed and plaid-direction perception between subjects was consistent for the two subjects tested and the limited conditions tested. This consistency supports the idea that contrast-induced misperception in plaid direction is merely a manifestation of a contrast-induced misperception of component speed.

The perception of relative speed is affected by the temporal presentation of the stimuli to be matched. Figure 8 shows the speed-matching data for three subjects (including one naive) when the gratings to be matched are presented simultaneously (open squares) or when two pairs of gratings, presented sequentially 500 ms apart, are matched (solid squares). All stimulus intervals, in both conditions, contain pairs of grating patches with the same perifoveal spatial arrangement (above and below fixation). In the simultaneous condition, the speed match was made between the two patches in the same single stimulus interval (as was done in all speed-matching experiments described above). In the sequential condition, both grating patches within a single interval moved at the same speed and the speed match was made between the two intervals. For all three subjects, the contrast-induced misperception of relative speed was less severe in the sequential condition. Subject LS actually made veridical matches under the sequential condition (figs. 8(b) and 8(e)). Furthermore, subjects PT and JL showed large reductions in their contrast-induced errors when the stimuli were presented sequentially. Therefore, the temporal presentation of two grating patches affected their perceived relative speed with gratings presented separately in time being more veridically matched.

Discussion

Contrast-Induced Misperception of Grating Speed

In this study, we have shown that when two horizontal gratings moving upward at the same speed within adjacent stationary windows are presented simultaneously, the lower-contrast grating appears to move more slowly by up to 50%. This effect is evident over a wide range of contrasts (2.5 – 50%) and is not accompanied by any systematic changes in uncertainty. The effect is a function of contrast ratio alone and is independent of the absolute

contrast level, except possibly at very low contrasts, with incomplete saturation at 50%.

Contrast effects on perceived speed have been documented previously by Thompson (1982), but his study was different in two ways: he only examined contrasts at and below 17.8% and he used the method of adjustment and magnitude estimation. Thompson found that lower contrast gratings appear to move more slowly only at temporal frequencies below 8 Hz. He reported that the effect becomes smaller with increasing temporal frequency and even reverses at temporal frequencies above 8 Hz. However, we found no evidence of this. In fact, for all three subjects examined at multiple temporal frequencies, the effect was still robust with lower contrast gratings appearing slower at 8.25 Hz. We did find that the task became very difficult for one subject and impossible for another at temporal frequencies at or above 10 Hz. This suggests that, at high temporal frequencies, subjects do not have a consistent percept of speed. The apparent reversal found previously is therefore probably an artifact of the experimental method with subjects making *speed* matches based on some other criterion. With our two-alternative forced-choice staircasing procedure, we report the point of subjective equality only if it is located on a clear psychometric curve with measured precision. The methods of adjustment and magnitude estimation generate apparent matches, regardless of whether the underlying matching performance is well behaved (i.e., is a sigmoidal function of test speed).

The fact that speed perception is dependent on contrast suggests that speed discrimination should be degraded by random large fluctuations in contrast. Any changes in contrast would be perceived as perturbations in speed and would therefore add to the observed uncertainty. However, McKee, Silverman, and Nakayama (1986) showed that randomization of contrast did not adversely affect speed discrimination. This apparent discrepancy with our present results can be resolved by our finding that the temporal presentation of the stimuli to be compared is important. At a fixed interstimulus interval (ISI) of 500 ms, subjects showed either a reduced or non-existent effect of contrast on perceived relative speed. McKee, Silverman, and Nakayama (1986) used the method of single stimuli that, like our sequential condition, presented stimuli one at a time. Their experiments were self-paced, so it seems reasonable to assume that the ISI under such conditions exceeded 500 ms; therefore, given our results, little or no effect would be expected. Another possible explanation for the discrepancy is that McKee and colleagues used foveal presentation while we used perifoveal presentation.

The magnitude of the difference between our simultaneous and sequential conditions varied for each subject. In fact, one subject actually made veridical matches when stimuli were presented sequentially. Given the results of McKee, Silverman, and Nakayama (1986), it would be interesting to know whether, at sufficiently long ISIs, all subjects would have made veridical matches. Further studies are needed to elucidate the time course of the putative washing out of the contrast-induced speed matching errors.

The spatial arrangement of our sequential stimulus (two patches moving at same speed) was unusual in order to match the exact spatial arrangement of the simultaneous stimulus. Unfortunately, subjects could have paid attention to or even looked at (although told to fixate on the center cross) one of the patches in a given interval since its motion contained all the necessary information to make the match with the second interval. However, the results in figure 7 suggest that the simultaneous-sequential difference is not due to foveal versus perifoveal viewing because in this (fig. 7) and a previous study (Stone, Watson, and Mulligan 1990) errors in perceived plaid direction were observed when the components had different contrast—even with foveal viewing. To resolve this issue, a systematic study of the effect of eccentricity on contrast-induced speed misperception will be necessary.

Plaid Motion

In a previous study, Stone, Watson, and Mulligan (1990) showed that when a moving plaid consists of components with different contrasts, its direction is misperceived with a bias in the motion direction of the higher contrast grating. They suggested that this bias was due to a reduction in perceived speed of the lower contrast component. In our study, we explicitly tested this by measuring perceived relative component speed and plaid direction in the same subjects under similar conditions. These results, and a similar recent finding by Kooi (1990), suggest that both the contrast induced plaid direction and grating-speed misperception are manifestations of the same underlying mechanism. Adelson and Movshon (1982) hypothesized that plaid motion is determined using a two-stage mechanism. First, the plaid is decomposed into the motion of the individual components. Second, plaid velocity is reconstructed using the intersections of constraints rule (Fennema and Thompson 1979). The data presented in figure 7 provide direct evidence for the hypothesis proposed by Stone, Watson, and Mulligan (1990) that the contrast-induced misperception of component motion is fed through the intersection of constraints rule to yield the misperception in plaid direction.

A striking difference between the previous plaid and our present grating results is that Stone, Watson, and Mulligan (1990) documented contrast induced misperceptions in plaid direction only at low contrast, but the contrast induced mismatches in grating speed shown here occur over, potentially, the entire range of contrasts. Thompson (1982) explored perceived grating speed only at the low end of the contrast scale so Stone, Watson, and Mulligan (1990) did not identify this conflict. However, this puzzling discrepancy can be resolved by noting that the saturation apparent in plaid-direction judgments occurs with nonparallel grating components while the lack of saturation apparent for grating-speed matching occurs with parallel gratings. In fact, when subjects were asked to match nonparallel gratings, their performance showed signs of contrast saturation sufficient to explain the plaid-direction results for both subjects tested despite the considerable differences between the two subjects.

The intersubject variability provides further evidence for the two-stage hypothesis (Adelson and Movshon 1982) because the plaid and grating paradigms yield consistent results throughout subjects. The subject who speed-matched orthogonal gratings veridically showed little or no plaid-direction error for plaids consisting of orthogonal gratings. The subject who showed a significant misperception of relative speed of orthogonal gratings also misperceived plaid direction. Why there should be such intersubject variability is unclear. However, the variability in orientation effect on the contrast-induced grating-speed misperception may underlie the considerable intersubject variability in the orientation effect on the contrast-induced plaid-direction misperception shown previously (Stone, Watson, and Mulligan 1990).

Because the effect of relative orientation on plaid and grating perception is so variable, further studies will be required for quantitative analysis. One possible explanation for the variability in speed-matching of orthogonal gratings is that, because we used circularly symmetric apertures in the orthogonal condition, the stimuli were smaller and therefore less salient than in the parallel conditions. Furthermore, the smaller size could have contributed to the change in the contrast effect for orthogonal gratings. We believe size is unlikely to have been entirely responsible because orientation dependence of contrast effects on plaid-direction perception was seen here (fig. 7) and in a previous study (Stone, Watson, and Mulligan 1990) despite using stimuli that were larger than those used to document the strong contrast effect on the speed matching of parallel gratings (fig. 2).

Despite the smaller size of the grating stimuli and the different spatial arrangement for the plaids and gratings, our predictions of plaid-direction errors are surprisingly

accurate. For grating-speed perception, the gratings must be nonoverlapping and, therefore, perifoveal to be symmetric. For plaid-direction perception, the gratings must be overlapping (and presented foveally for convenience). Because it is not possible to design an experiment where the spatial arrangements are identical and because this comparative approach merely provides a quantitative correlation between two phenomena and can never provide a causal link, a more precise examination was unwarranted.

A number of other studies has recently found that variables that affect grating-speed perception also affect plaid-direction perception in a manner consistent with the two-stage hypothesis (Adelson and Movshon 1982). Using an adapting grating to reduce the apparent speed of a single component (Derrington and Suero 1991) or using a plaid consisting of gratings of different spatial frequencies (Kooi 1990; Smith and Edgar 1991) also yields directional errors consistent with a component-driven analysis. Although no actual causal link has been established, these results, together with speed and direction discrimination studies (Welch 1989; Stone 1988, 1989, 1990), and the results presented here, show that in a wide number of circumstances plaid-motion perception is consistent with a component-driven mechanism using the intersections of constraints rule to reconstruct pattern (plaid) motion from component motion. However, some studies have recently found that, for some plaid angle configurations, plaid motion is not consistent with a two-stage component-driven model, leading to the suggestion that other mechanisms may also be at work (Ferrera and Wilson 1987, 1990; Stone 1988; Derrington and Badcock 1990).

Speed Perception

The question of whether humans perceive speed directly or whether speed is derived from other sources has been addressed in a number of studies (Lappin et al. 1975; McKee 1981; Orban, de Wolf, and Maes 1984). They proposed that perceived speed is unlikely to be derived from distance or duration perception because speed discrimination is better than distance or duration discrimination. However, there is evidence to suggest that size and distance traveled does affect perceived speed (Brown 1961; Katz et al. 1990). McKee, Silverman, and Nakayama (1986) used the same discrimination argument to suggest that speed perception is not derived from temporal frequency. This latter result is, however, unconvincing because one of the two subjects showed an equal ability to discriminate small differences in either speed or temporal frequency. Furthermore, the lack of physiological evidence for a clear representation of speed anywhere

within visual cortex (Maunsell and Newsome 1987) suggests that speed may be inferred from other measures. The issue of the primary nature of speed perception remains unresolved.

A second related issue is whether or not humans perceive speed veridically. The concept that speed is veridically perceived was supported by the results of McKee and others (1981, 1986) who showed that random perturbations of duration, distance traveled, and spatial and temporal frequencies do not have a significant effect on speed discrimination. They did, however, show a small effect of spatial frequency on perceived speed with higher spatial frequencies perceived as faster. Ferrera and Wilson (1990) have also found this, although their effect was much larger. Smith and Edgar (1990), however, found the converse. This apparent discrepancy can be resolved by noting that when two gratings were presented simultaneously, the lower spatial frequency grating appears slower (Smith and Edgar 1990) and, when stimuli are presented sequentially, the higher spatial frequency gratings appear faster (Ferrera and Wilson 1990; McKee, Silverman, and Nakayama 1986; Diener et al. 1976; Campbell and Maffei 1981). The grating-speed results are consistent with the finding that the perceived direction of moving plaids composed of components of different spatial frequency is biased in the direction of the lower spatial frequency component (Kooi 1990; Smith and Edgar 1991). These results complement those presented here and provide a convincing ensemble of data that demonstrates that speed is not veridically perceived in a wide set of situations. Furthermore, they provide additional evidence that simultaneously and sequentially presented moving stimuli are processed differently, although a foveal versus perifoveal difference cannot be ruled out.

Speed Coding within Visual Cortex

From the physiology and anatomy of monkey visual cortex, it appears that direction and speed information are represented in fundamentally different ways. Direction information appears to be coded within a place map in which there is a systematic representation of each possible direction of motion in an orderly array of cortical columns within MT (Albright, Desimone, and Gross 1984). Presumably, perceived direction of motion is extracted by determining which direction column is the most active. A recent study has, in fact, shown that localized electrical stimulation, presumably within a single direction column, biases direction judgments in the direction of the column (Salzman, Britten, and Newsome 1990). Although contrast affects the absolute level of neuronal activity in both striate cortex and MT neurons (Sclar, Maunsell, and Lennie 1990; Albrecht and Hamilton 1982), the spatial

distribution of activity is most likely robust to the contrast level.¹ Nakayama and Silverman (1985) found that, indeed, direction discrimination, as measured by the minimum motion necessary to discriminate direction, was unaffected by increases in contrast above about 3%. The ability to determine the direction of motion is therefore thought to saturate at very low contrast.

The coding of speed information is poorly understood and is likely to be different. Directionally selective cortical neurons are tuned for speed but, unlike direction (Albright, Desimone, and Gross 1984), orientation (Hubel and Wiesel 1968; Hubel, Wiesel, and Stryker 1978), ocular dominance (Hubel and Wiesel 1968; Hubel and Wiesel 1974; Wiesel, Hubel, and Lam 1974; Tootell et al. 1988a), or even spatial frequency (Tootell et al. 1988b), there is no apparent spatial organization for speed tuning. Therefore, how speed is coded remains an open question, although speed cannot be coded in the firing rate of individual neurons (no such cells have been found in the visual cortex) nor by a place code. One possibility is that speed is coded in the firing rate of a set of neurons. However, firing rate is very sensitive to contrast in both striate cortex and MT (Albrecht and Hamilton 1982; Sclar, Maunsell, and Lennie 1990). This problem could be remedied by taking ratios of the firing rates of different neurons. If the contrast sensitivities were equal, any contrast effect would be cancelled. A ratio scheme of this type has been proposed for velocity coding by Harris (1980) and it gains some plausibility from psychophysical evidence suggesting just two populations of speed-tuned cells, one preferring slow rates of movement (below 4 Hz) and the other faster rates (Watson and Robson 1981; Thompson 1983).

The problem of contrast and speed coding has been of particular concern to theoreticians who have postulated that the visual system uses linear oriented spatio-temporal filters to extract motion information because such filters are sensitive to changes in contrast (Watson and Ahumada 1983). One solution to this problem would be to use the temporal frequency of the filter's output modulation, a measure that is independent of contrast (Watson and Ahumada 1985). However, this assumes that temporal frequency is veridically encoded independent of contrast. Another approach would be to use motion energy (Adelson and Bergen 1985; Heeger 1987), a phase-independent measure derived from the output of the linear spatio-temporal filters, but motion energy is proportional to the square of contrast. Therefore, in order to yield a

contrast-independent measure of speed, motion energy must first be divided (normalized) by another energy signal with the same contrast sensitivity. Specifically, one can take the difference between the outputs of rightward and leftward motion energy sensors and divide that by the *stationary* energy to yield a true speed signal (Adelson and Bergen 1986). However, the critical issue remains what signal is actually used as the *stationary* energy.

A potential neuronal implementation would be to normalize the output of striate cortical complex cells, postulated to encode motion energy (Emerson, Bergen, and Adelson 1992), with an *average-contrast* signal constructed by pooling the output of all complex cells over a range of orientation and spatial frequencies and over a wide spatial area (Heeger 1991). If the area over which the pooling is done is large enough to encompass both patches of our stimuli while the motion energy associated with the patch is detected over a smaller spatial extent, then the signal detected by the higher contrast grating would be normalized by an inappropriately low average contrast. Conversely, the motion energy generated by the lower contrast grating would be normalized by an inappropriately high average contrast. Thus, a contrast-normalized motion-energy scheme can qualitatively explain the observed contrast-induced misperception of relative speed.

This scheme can be extended to explain our additional findings. If the contrast is normalized by a signal pooled only over similar orientations/directions, then two orthogonal gratings would be normalized largely independently. This could explain why the contrast effect is dependent on the relative orientations/directions of the gratings with a tendency to be weaker for orthogonal gratings. The normalization in the orthogonal case might be more correct since the two different energy signals from the two patches would only partially interfere with each others' normalization. Further experiments examining the entire range of relative orientations are needed to determine the role of orientation in this putative normalization process.

The normalization scheme can also explain the fact that the perceived relative speed of simultaneously presented gratings is more contrast dependent than that of two sequentially presented gratings: the normalization takes place over a finite time. Two gratings presented sequentially would be normalized separately. The normalization in the sequential case would be more correct since the two different energy signals from the two intervals would only partially interfere with each others normalization. Further experiments examining a wider range of ISIs are needed to determine the temporal extent of the putative normalization process.

¹This is only true above some minimal contrast level necessary to recruit most neurons. In MT, most neurons are firing at half-maximum by about 10% (Sclar, Maunsell, and Lennie 1990).

A third experiment that could be used to examine the normalization hypothesis would be to determine whether the distance between the grating patches is important. The normalization hypothesis predicts that speed-matching should become more veridical with increased distance. Experiments examining a range of interpatch distances are needed to determine the spatial extent of the putative normalization process.

A more specific model of contrast normalization must be developed to predict quantitatively our results, particularly the finding that perceived relative speed is a quasilinear function of log contrast ratio. However, there is other empirical evidence for this quantitative relationship between speed and contrast. Using an induced-motion paradigm, Raymond and Darcangelo (1990) recently found a similar interaction between perceived speed and contrast. They moved a variable-contrast surround grating to impart apparent motion in the opposite direction to a stationary center grating. The induced speed was a quasilinear function of the surround contrast up to 60% contrast. However, they found that changing the center contrast had no effect. Despite this apparent contradiction, their second result is entirely consistent with our results and the contrast-normalization model. The motion energy of their center stimulus was always zero because the center was stationary, so its contrast is irrelevant.² Furthermore, in a preliminary report, Rubin and Legge (1981) showed that the relative latency of adjacent drifting gratings was misperceived in a manner consistent with their relative speed being a linear function of log contrast ratio over the entire range of contrasts (tested up to 80%). Finally, Chubb, Sperling, and Solomon (1989) have shown that the perceived contrast of a texture patch is influenced by the contrast of the surrounding texture. Although this is not a motion phenomenon, it demonstrates the existence of another type of contrast normalization similar to the one proposed here, particularly since their phenomenon appears to be orientation specific (Solomon, Chubb, and Sperling 1990).

Conclusion

Our results show that the human visual system is only partially successful in its endeavor to extract speed independently of contrast. These results, together with a large body of recent studies, show that speed is often not veridically perceived and is a function of a number of other factors—most notably contrast and spatial frequency (Diener et al. 1976; Campbell and Maffei 1981; Stone, Thompson, and Watson 1990; Kooi 1990; Smith and

Edgar 1990, 1991; Ferrera and Wilson 1991). Furthermore, these contrast effects may manifest themselves during real world navigation situations such as flying or driving through smoke, fog, or shadows, or over low-contrast terrain like water or sand, or if pilots use night-vision equipment that produces low-contrast imagery. If contrast causes image speed to be misperceived, then forward speed may be misperceived. In addition, because veridical extraction of self-motion information generally requires accurate image-speed information, heading direction and environmental layout may be misjudged. Our results, therefore, put new constraints on models of human motion perception, provide additional insight into how the cortex processes visual motion, will help in the development of more realistic models of human performance in visually-guided tasks, and can ultimately provide important information to those designing visual display systems to be used during navigation or in flight simulators.

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²This is exactly true only given appropriately narrow tuning of the underlying spatio-temporal filters.

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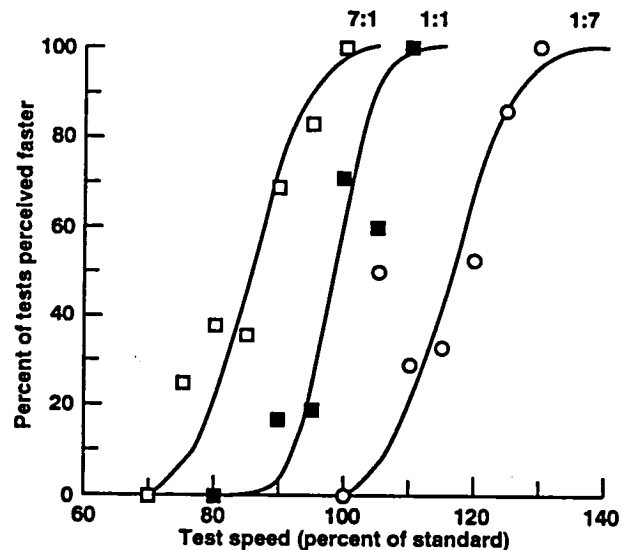


Figure 1. Raw psychometric curves for one subject at three contrast ratios. The data are plotted as the percent of trials in which the test grating was perceived faster than a 2°/sec standard as a function of the actual speed of the test. All gratings were 1.5 c/d unless otherwise stated. The solid lines are integrals of Gaussians fitted using probit analysis, a weighted least-square method that weighs each point according to the number of trials at that test speed and according to the binomial distribution of the underlying probability.

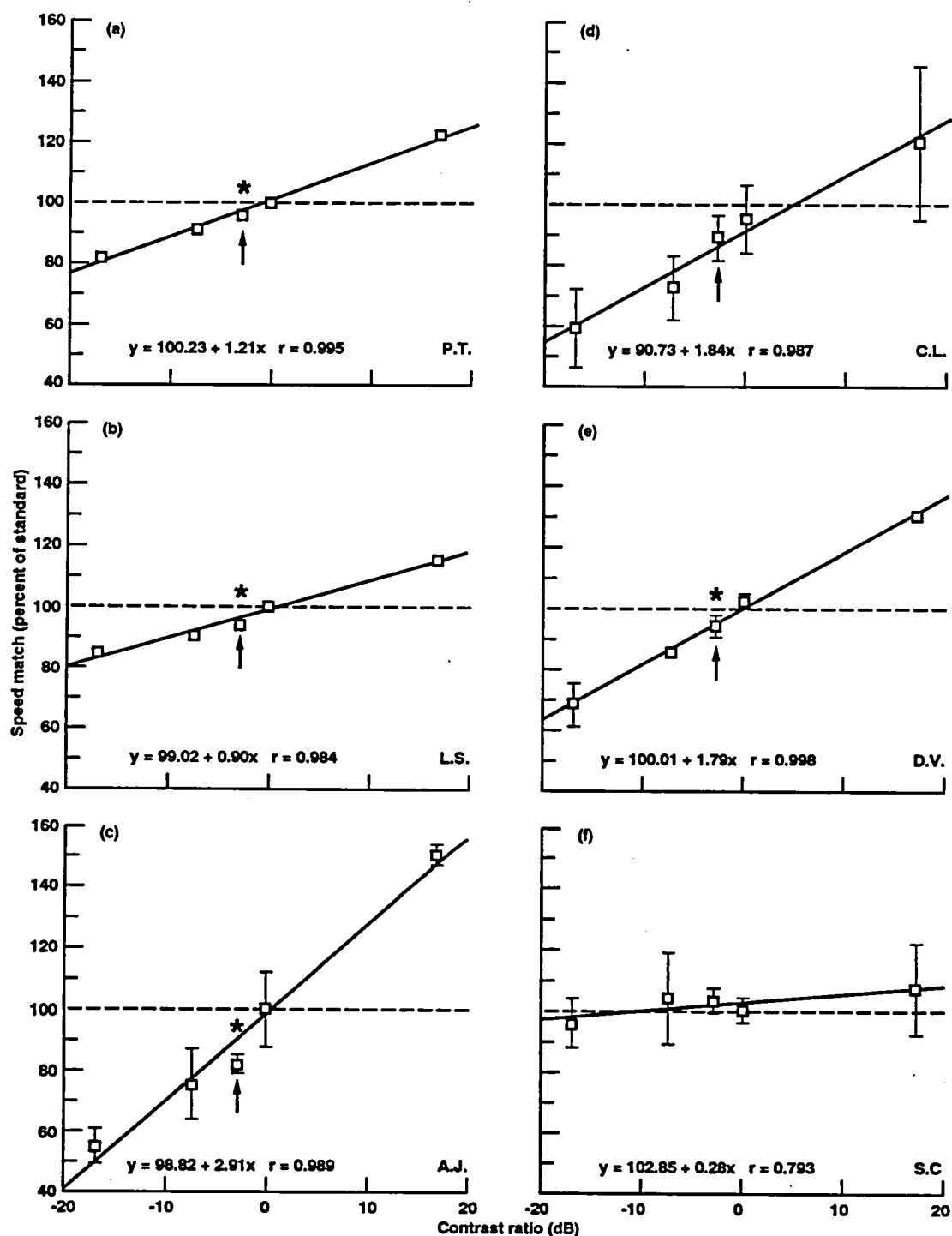


Figure 2. Speed matches of six subjects. The mean inflection points of fitted Gaussians are plotted as a function of the contrast ratio. The error bars are standard deviations over three sessions. The dashed line represents veridical matching. The solid lines, whose equations appear at the bottom of each panel, were fit to the data using simple linear regression. Asterisks indicate the 50% contrast standard points with significant mismatches ($p < 0.05$).

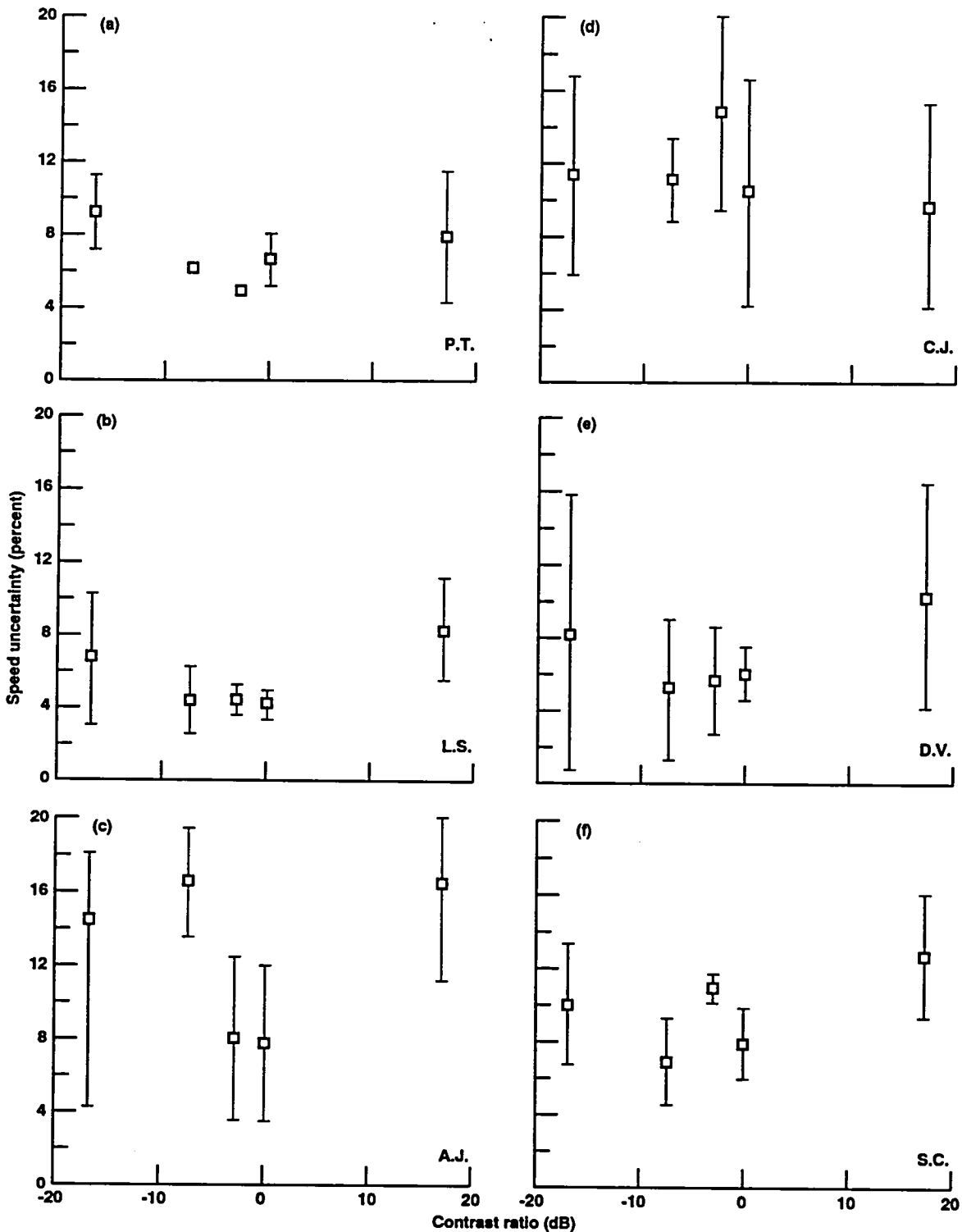


Figure 3. Speed discrimination for the same six subjects and same conditions as in figure 2. Speed uncertainty was defined as the ratio of the standard deviation of the fitted Gaussian to the standard speed divided by $\sqrt{2}$ because the performance variance is assumed to be the sum of the two equal variances produced by uncertainty in both the test and standard speeds. The mean uncertainty is plotted as a function of the contrast ratio. The error bars are standard deviations over three sessions.

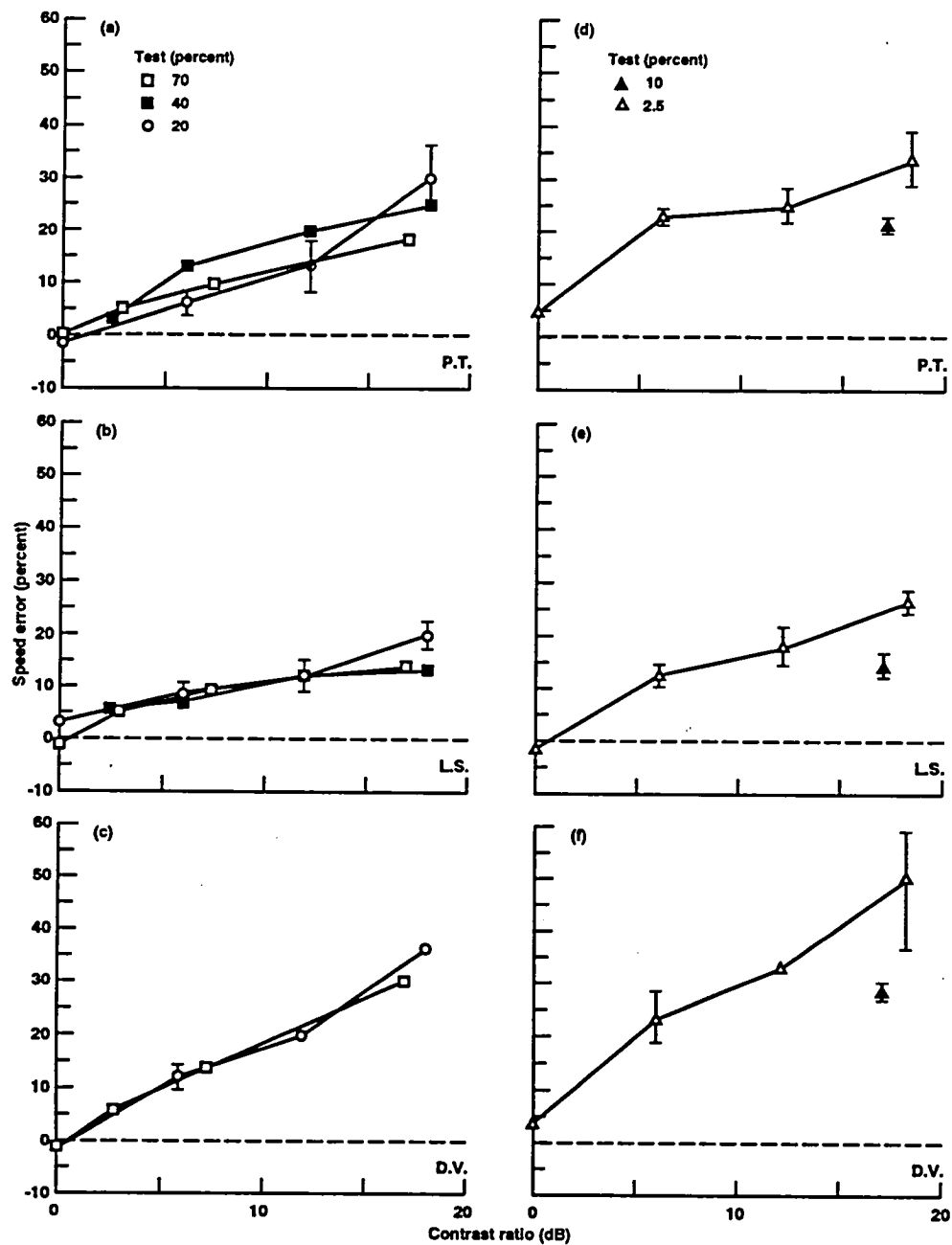


Figure 4. Contrast-induced speed errors are independent of absolute contrast. Mean speed error over three sessions is plotted as a function of the contrast ratio for high contrast tests matched to lower contrast standards (abc) and for low contrast tests matched to higher contrast standards (def) for three subjects. For clarity, standard deviations are only plotted for the 2.5% and 20% contrast test conditions. The dashed line represents veridical matching. The 70% and 10% contrast test data are replotted from figure 2. The 40% test data were generated by matching to 5, 10, 20 and 30% contrast standards. The 20% and 2.5% contrast test data were generated by matching to 2.5, 5, 10, and 20% contrast standards.

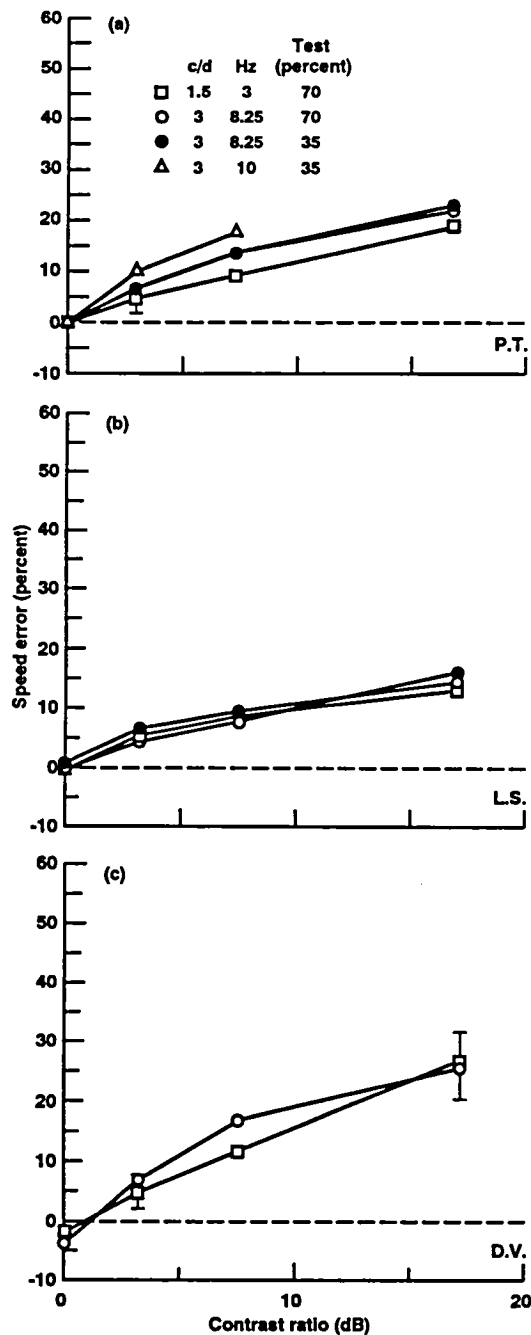


Figure 5. Contrast-induced speed errors are insensitive to changes in temporal/spatial frequency. Mean speed error over three sessions is plotted as a function of the contrast ratio for different spatial/temporal frequencies and test contrasts for three subjects. For clarity, standard deviations are only plotted for the 1.5 c/d condition. The dashed line represents veridical matching.

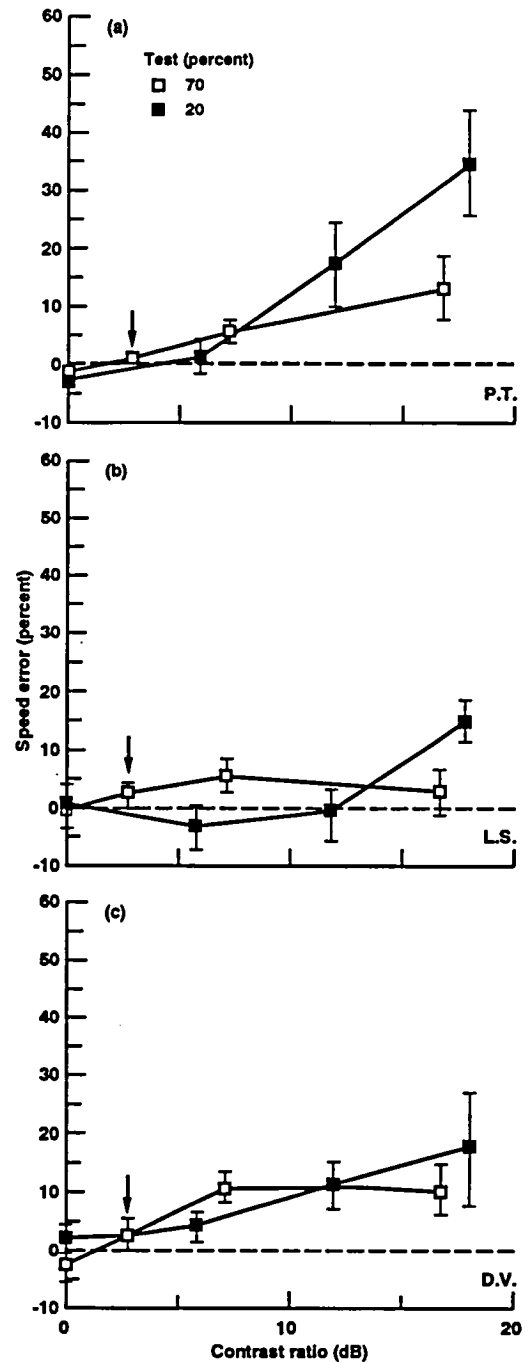


Figure 6. Contrast-induced speed errors for orthogonal gratings. Mean speed error is plotted as a function of the contrast ratio for two different test contrasts using orthogonal gratings for three subjects. The error bars are standard deviations over three sessions. The dashed line represents veridical matching.

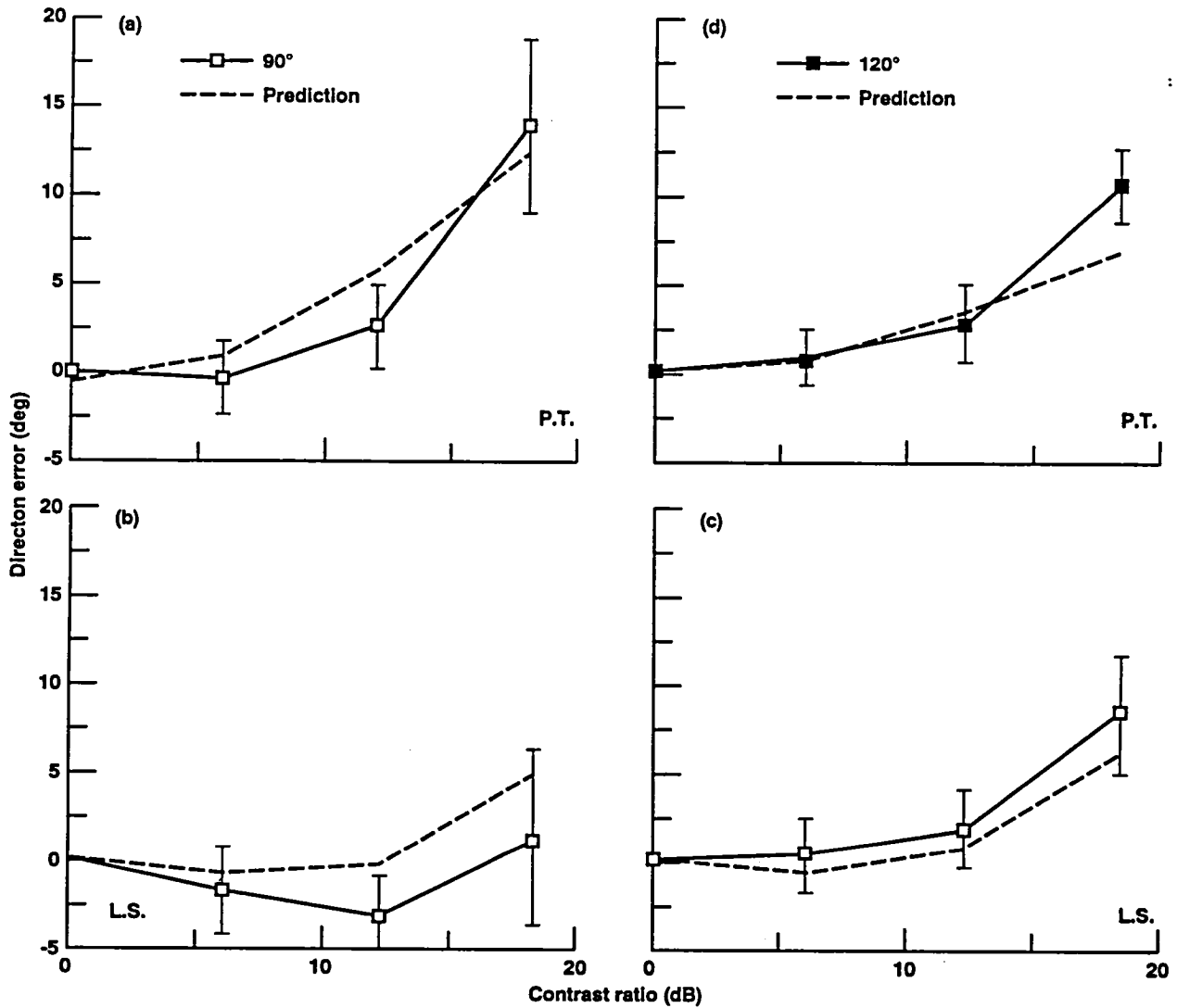


Figure 7. Contrast-induced grating-speed errors explain contrast-induced plaid-direction errors. Mean plaid-direction errors (squares) are plotted as a function of contrast ratio at two different relative orientations for two subjects. Error bars are mean uncertainty (standard deviation of the fitted Gaussian) over three sessions. The dashed lines represent simulated plaid-direction errors using equation (1) and measured grating-speed errors in the same subjects.

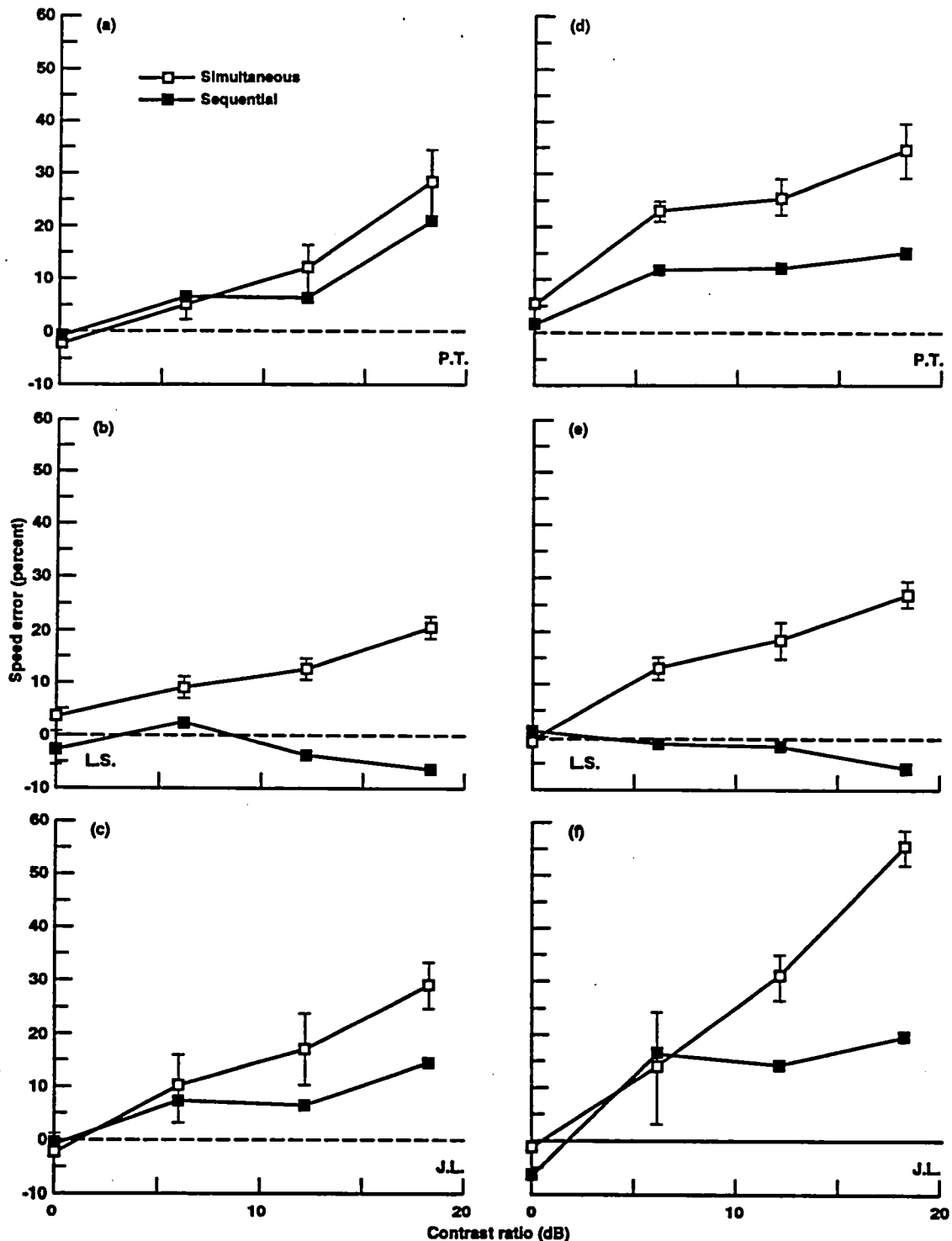


Figure 8. Contrast-induced speed errors are weaker with sequential presentation. Mean speed errors are plotted as a function of contrast ratio using both simultaneous (open square) and sequential (solid square) presentations. The error bars are standard deviations over three sessions and, for clarity, are only presented for the simultaneous condition. The dashed line represents veridical matching. The lefthand panels show the data generated by slowing a 20% contrast test grating to match 20, 10, 5, and 2.5% contrast standards. The righthand panels show the data generated by speeding up a 2.5% contrast test grating to match 20, 10, 5, and 2.5% contrast standards.

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13. ABSTRACT (Maximum 200 words) This study is part of an ongoing collaborative research effort between the Life Science and Human Factors Divisions at NASA Ames Research Center to measure the accuracy of human motion perception in order to predict potential errors in human perception/performance and to facilitate the design of display systems that minimize the effects of such deficits. The study describes how contrast manipulations can produce significant errors in human speed perception. Specifically, when two simultaneously presented parallel gratings are moving at the same speed within stationary windows, the lower-contrast grating appears to move more slowly. This contrast-induced misperception of relative speed is evident across a wide range of contrasts (2.5 - 50%) and does not appear to saturate (e.g., a 50% contrast grating appears slower than a 70% contrast grating moving at the same speed). The misperception is large: a 70% contrast grating must, on average, be slowed by 35% to match a 10% contrast grating moving at 2°/sec (N = 6). Furthermore, it is largely independent of the absolute contrast level and is a quasilinear function of log contrast ratio. A preliminary parametric study shows that, although spatial frequency has little effect, the relative orientation of the two gratings is important. Finally, the effect depends on the temporal presentation of the stimuli: the effects of contrast on perceived speed appears lessened when the stimuli to be matched are presented sequentially. These data constrain both physiological models of visual cortex and models of human performance. We conclude that viewing conditions that effect contrast, such as fog, may cause significant errors in speed judgments.					
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